
THE POLLEN OF *TAKHTAJANIA PERRIERI* (WINTERACEAE)¹

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ABSTRACT

Pollen morphology and ultrastructure of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy, the Malagasy member of the Winteraceae, were studied and compared with pollen of other members of this primitive angiosperm family. Pollen is in permanent tetrahedral tetrads, which are the largest in the family. As in *Drimys* and *Pseudowintera*, the apertures are expanded into protuberant papillae, suggesting premature commencement of growth of the pollen tubes. Apertures are circular or slightly oval, and it is concluded that previous reports of colpate and trichotomocolpate (trichotomosulcate) apertures, based on the study of dried material from the type specimen, are incorrect. The exine is reticulate and tectate-columellate and most columellae have characteristic expanded bases where they join the foot layer. Beneath the foot layer is an endexine and an intine, which is two-layered in apertural areas, as in other Winteraceae. As in some other genera, the aperture is surrounded by an annulus, with an underlying thickened endexine consisting of tangentially aligned lamellae. The septal exine is highly reduced, and small gaps in the ectexine are plugged with endexine, suggesting that pollen mitosis is asynchronous within a tetrad, as in *Pseudowintera* and *Drimys*, but in contrast to *Belliolum*, *Bubbia*, *Exospermum*, *Tasmannia*, and *Zygogynum*, in which these gaps remain or are blocked by the deposition of intine after pollen mitosis. On the basis of its pollen morphology, *Takhtajania* seems most closely related to *Drimys* and *Pseudowintera*.

Key words: *Bubbia perrieri*, flora of Madagascar, Magnoliidae, pollen morphology, *Takhtajania*, tetrad pollen, Winteraceae.

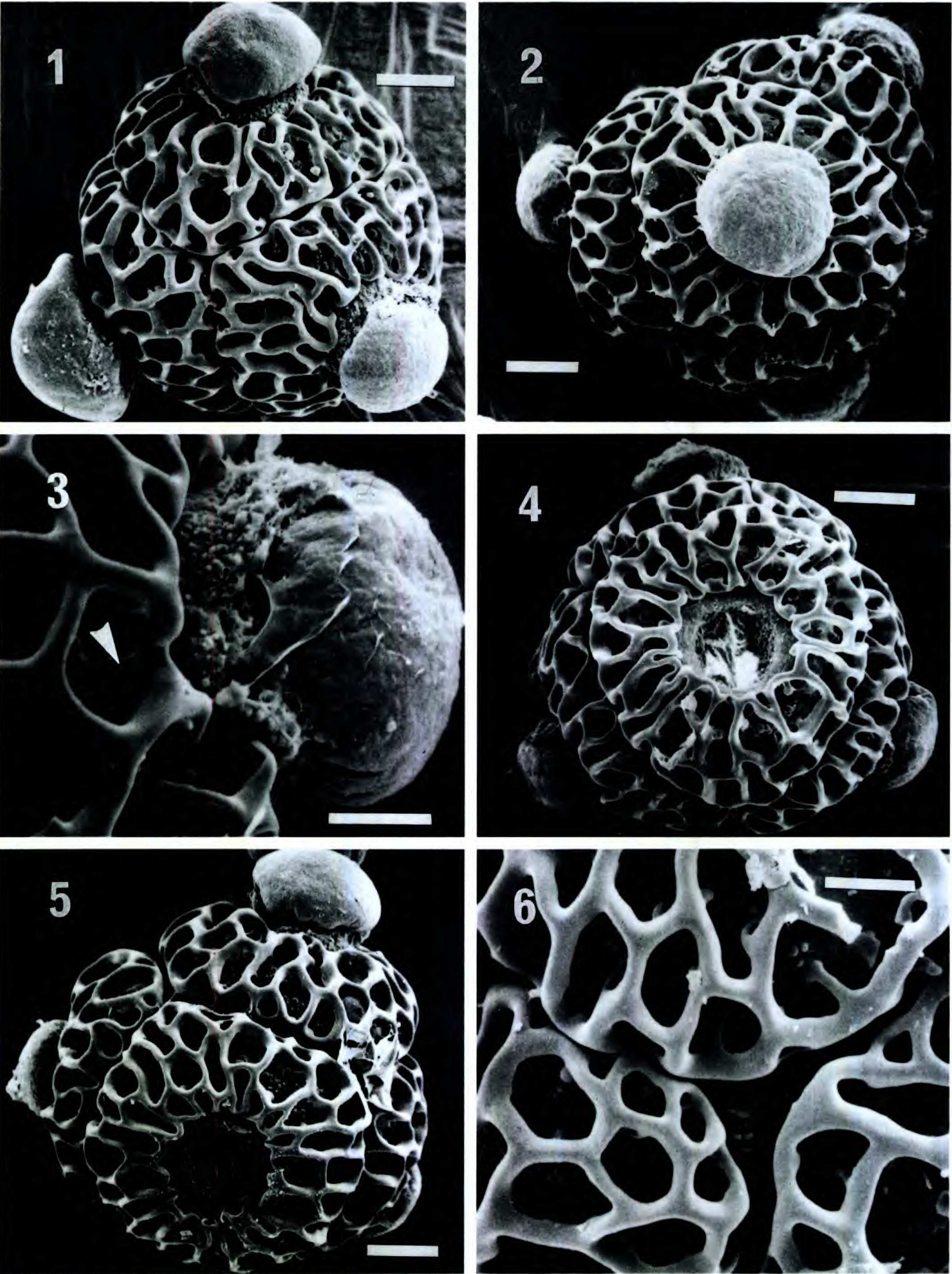
The rediscovery of *Takhtajania perrieri* (Schatz et al., 1998) has provided the opportunity to study liquid-preserved polliniferous material for the first time. Although there have been three quite detailed studies of the pollen of this plant (Straka, 1963; Lobreau-Callen, 1977; Praglowski, 1979), they were based on dried material from the type specimen, collected nearly 90 years ago. These three authors disagreed on the interpretation of some aspects of the pollen of *Takhtajania*.

Takhtajania pollen is in permanent tetrahedral tetrads, a feature that occurs in all other members of the Winteraceae, with the exception of four species of *Zygogynum*, which have monads (Sampson, 1974; Praglowski, 1979; Vink, 1993). Monad pollen in these *Zygogynum* species seems to have evolved from the tetrad condition (Sampson, 1981; Doyle et al., 1990a, b). Previous studies on the pollen of *Takhtajania* indicated that its pollen tetrads are larger than those of other Winteraceae. It has been claimed, too, that a few apertures of *Takhtajania* are of the trichotomosulcate type, with a three-slit sulcoid aperture, in contrast to the invariably round or oval apertures of other members of the family.

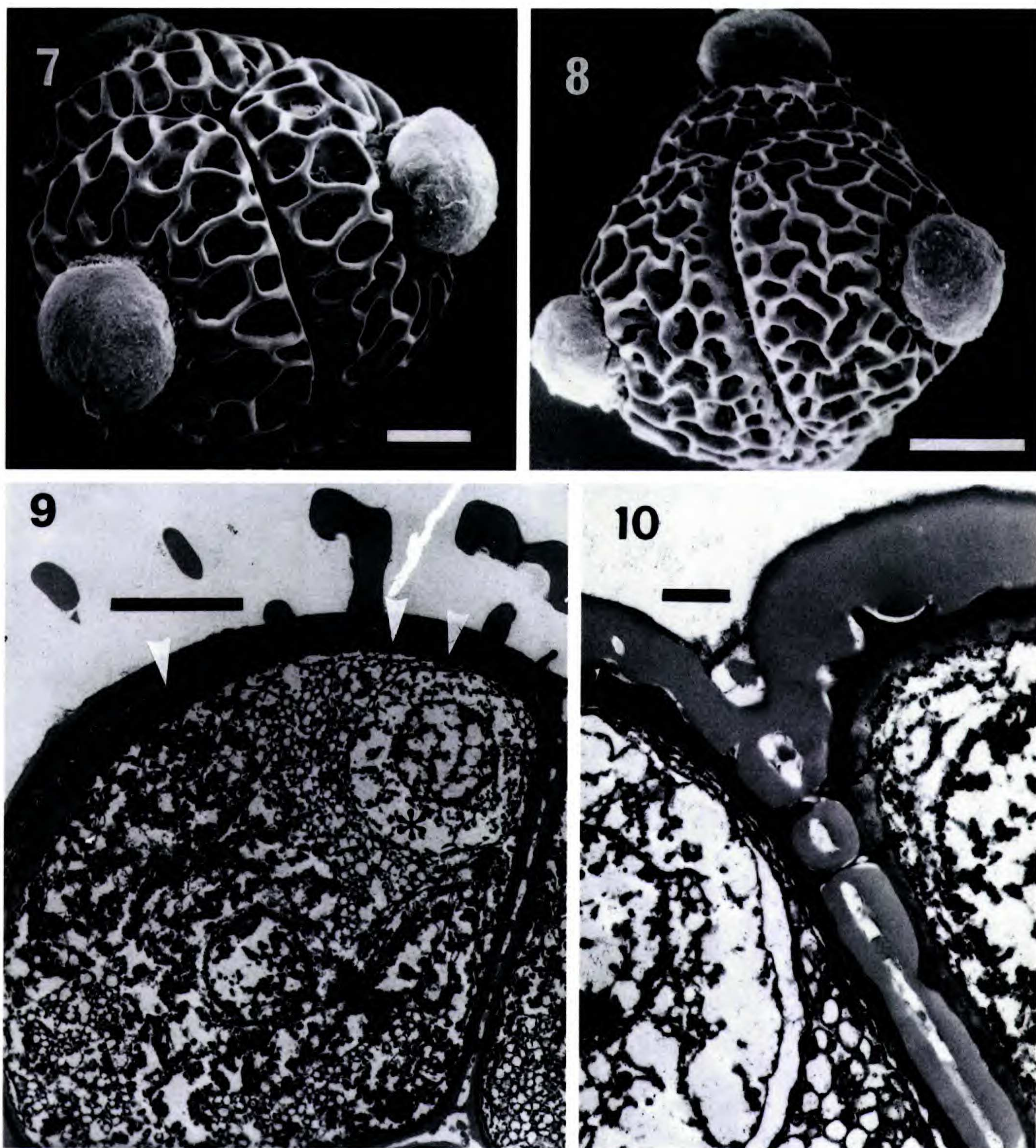
The present study was undertaken, therefore, to provide further information and illustrations of the pollen of *Takhtajania* based on liquid-preserved material. This will enable further comparisons to be made with the pollen of other genera of Winteraceae, which were studied in detail by Praglowski (1979). It should be noted that the material used in the present study was obtained about 150 km southeast of the original type collection. This raises the slight possibility that some differences between pollen in previous and present studies may be the result, not only of dried versus preserved material, but also of differences between the two populations of *Takhtajania*. For as Smith (1943), Vink (1970), Ehrendorfer et al. (1979), and others have demonstrated, there can be considerable morphological variability between populations of some species in the Winteraceae. However, such differences have not been demonstrated for their pollen grains. Generic names used follow those of Praglowski (1979), except that as recommended by Smith (1969) *Tasmannia* is substituted for *Drimys* sect. *Tasmannia*. The merging of *Bubbia*, *Belliolum*, and *Exospermum* into *Zygogynum* (Vink, 1985) is therefore not followed in the present paper.

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Figures 1–6. *Takhtajania perrieri* (SEM micrographs). —1. Pollen tetrad showing three of the four protuberant apertural papillae (scale bar = 10 μm). —2. Pollen tetrad with the uppermost pollen grain in polar view and all four apertural papillae visible (scale bar = 10 μm). —3. Apertural region of a pollen grain in lateral view. Annulus region indicated by asterisk; white arrow shows expanded base of a columella (scale bar = 5 μm). —4. Pollen tetrad with a sterile pollen grain uppermost, which lacks a protuberant papilla, with the annulus surrounding the aperture in polar view (scale bar = 10 μm). —5. Pollen tetrad with a sterile pollen grain (lowermost) in which the aperture has become torn into a colpus-like shape (scale bar = 10 μm). —6. Center of a pollen tetrad with portions of three pollen grains visible (scale bar = 5 μm).



Figures 7–10. —7. *Takhtajania perrieri* (SEM): a pollen tetrad with apertural regions of two pollen grains (lower left and upper right) in semi-lateral view (scale bar = 10 μm). —8. *Pseudowintera colorata* (SEM): a pollen tetrad with approximately similar orientation to the previous figure (scale bar = 10 μm). —9. *Takhtajania perrieri* (TEM): section of part of a tetrad showing most of a pollen grain in non-median section passing through the external fringes of the annulus, with white arrows indicating the endexine, a black arrow indicating the intine, and an asterisk showing the cytoplasm of the generative cell, which has a central nucleus (scale bar = 5 μm). —10. *Takhtajania perrieri* (TEM): section of portion of a tetrad illustrating part of the external and internal boundary between two grains. The arrows indicate gaps in the extexine, which have been filled with endexine (scale bar = 1 μm).

MATERIAL AND METHODS

Flowers and flower buds of *Takhtajania perrieri* (Capuron) Baranova & J.-F. Leroy were collected (*P. J. Rakotomalaza et al. 1342*) on 13 June 1997 from the Anjanaharibe-Sud Special Reserve, Antsiranana, Madagascar, and fixed in FAA.

Mature and nearly mature pollen for scanning electron microscope (SEM) study was dehydrated in an ethyl alcohol/acetone series, critical-point dried, sputter-coated with a thin layer of gold, and examined with a Philips 505 SEM. Pollen for transmission electron microscope (TEM) study was post-fixed in 1% OsO_4 , dehydrated, embedded in Spurr's

resin, sectioned, and stained with uranyl acetate and lead citrate. Some mature pollen for light microscopy (LM) was acetolyzed and some was dehydrated in a TBA series, embedded in Paraplast, sectioned with a rotary microtome at 10 μm , and stained with haematoxylin, safranin, and fast green.

Measurements of external pollen features were based on LM using acetolyzed material to enable comparison with other genera of Winteraceae described in the pollen monograph of Pragłowski (1979); 50 tetrads were sampled.

For comparative purposes, pollen tetrads of *Pseudowintera colorata* (Raoul) Dandy, obtained from native forest, Brown Cow Ridge, N.W. Nelson, New Zealand (voucher *WELTU 12949*), were examined under SEM, with treatment and fixation as for *Takhtajania*.

RESULTS

EXTERNAL MORPHOLOGY

The most striking feature of the pollen tetrads of *Takhtajania*, which is shared by some other members of the family, is an expansion of the aperture, suggesting premature commencement of growth of the pollen tube (Figs. 1, 2). There is minor variation in the size of these "protuberant papillae" (Bailey & Nast, 1943) even between grains of the same tetrad, which may reflect differences in the degree of hydration of individual pollen grains. The surface of the aperture membrane is relatively smooth, in contrast to a surrounding verrucate (warty) annulus (Fig. 3). A few tetrads were observed in which one or more of the pollen grains did not show a bulging of the aperture (Fig. 4). Sections of tetrads revealed that such grains were sterile. Sometimes the aperture membranes of these pollen grains were torn (Fig. 5), with the ruptured part varying in shape.

The tetrads are of the acalymmate type (Van Campo & Guinet, 1961), "in which each individual pollen grain is encompassed by its own ectexine which is usually incompletely developed in the septal part" (Pragłowski, 1979: 4), as in other Winteraceae. Pollen grains are in tetrahedral tetrads, radially symmetrical, heteropolar, semitectate, and rounded to rounded-triangular in polar view (Fig. 2), uniaperturate with distal polar apertures, mostly round (ulcerate), although a few were oval. In lateral view, each pollen grain has a hemispherical distal (exposed) face (Fig. 1), excluding the shape of the apertural protrusion, and a proximal region, where the grain is joined to the other three members of the tetrad, consisting of three flattened inclined rather triangular surfaces converging near the "geometrical centre" of the tetrad. Pragłowski

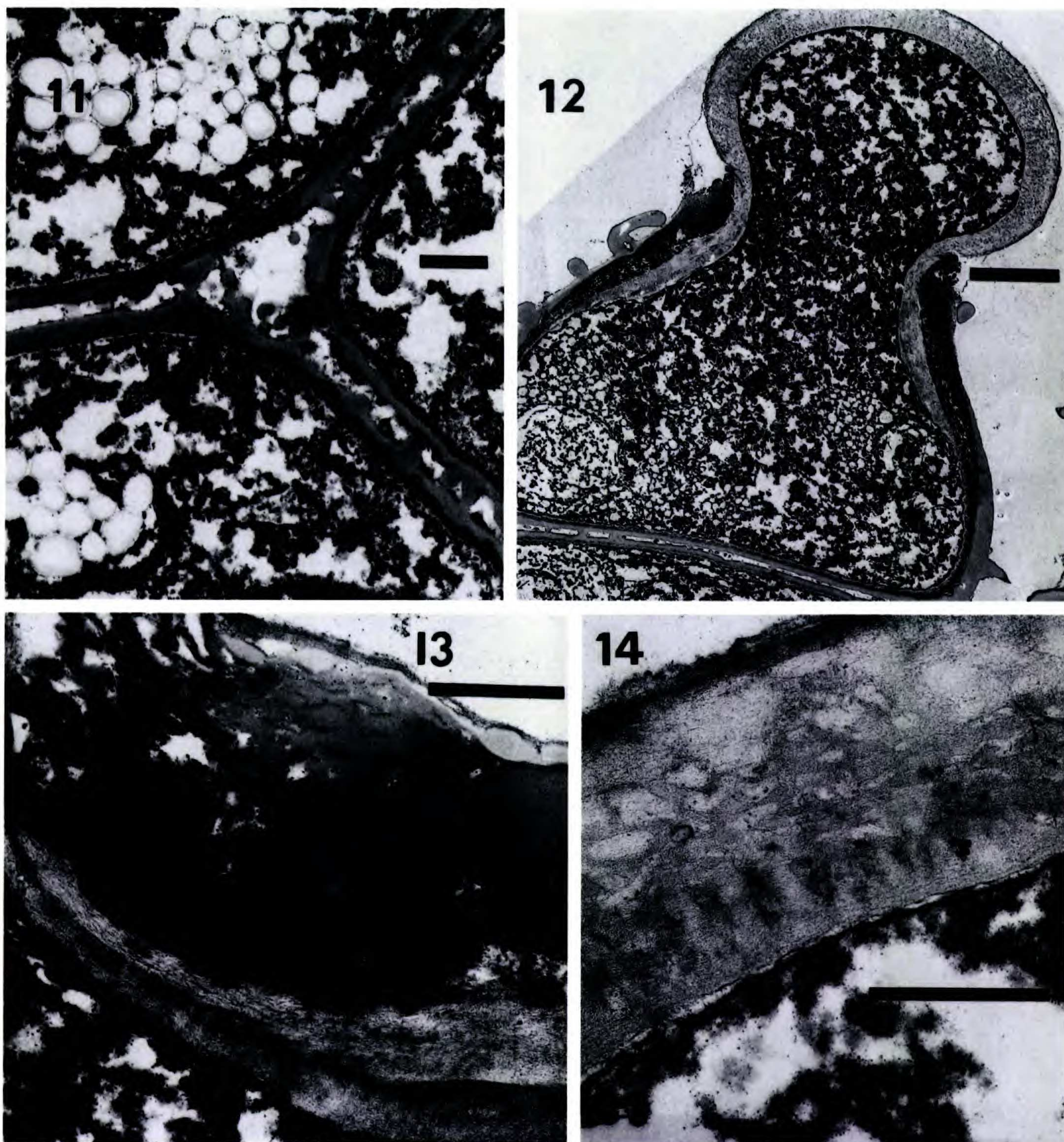
(1979: 4) defined this as "the point at the centre of the free space between four coalescing pollen grains of a tetrahedral tetrad."

Diameter of tetrads, excluding apertural protrusions, which are destroyed by acetolysis, 65–83 μm (mean 74 μm); polar axis of individual pollen grains 23–33 μm (28 μm); largest diameter perpendicular to the polar axis 50–60 μm (55 μm). More than 90% of the apertures examined were almost exactly circular with a diameter (including the surrounding annulus) of 13–25 μm (20 μm); mean diameter of apertures, excluding annulus, 12.5 μm . The few oval apertures observed ranged from $6 \times 10 \mu\text{m}$ to $8 \times 11 \mu\text{m}$. Width of annulus ca. 2.5–6 μm (Fig. 4).

The reticulum on exposed surfaces of the tetrads has mostly medium-sized lumina with shapes ranging from square, rectangular, or polygonal to oval, circular, and irregularly curved sinuous outlines (Figs. 1, 2, 4–7). Muri forming the reticulum are, therefore, straight or curved and not invariably winding, as Pragłowski (1979) found in pollen from herbarium material. As Pragłowski (1979) noted, there are about 25 to 30 lumina in a pollen grain seen in lateral view (Fig. 1). Some lumina are smaller near the borders between members of the tetrad (Figs. 1, 6, 7) and, as in all members of the family with tetrad pollen, the reticulum (or perforate tectum in *Exospermum*) is completely interrupted near where individual grains are fused (Figs. 1, 6, 7). Only unbranched columellae were observed supporting the muri. Lobreau-Callen (1977) noted that rarely the columellae are duplicolumellate, although Pragłowski (1979) commented this was not clearly confirmed. Columellae are cylindrical, not quite as wide as the muri, and they are usually splayed out at their proximal ends forming a rounded flattened cushion, which joins onto the foot layer (Figs. 3, 6). The outer surface of the foot layer is mostly smooth, but at intervals there are small, mostly spherical, ornamentations of varying size (Figs. 1–7). Thickness of the sexine was 4–6 μm and the nexine up to 1.5 μm , excluding thinner parts near the aperture of each pollen grain.

ULTRASTRUCTURE

Extraseptal ectexine is 5–7.0 μm thick, excluding thinner regions near apertures. Muri are elliptical to obovate in cross section and generally about 1.5 μm wide and 1.2–2.2 μm high, with a height/width ratio of 1:1 to 3:2. Columellae ca. 2–4 μm in height, i.e., as high as or higher than muri. In extraseptal parts, the foot layer is continuous except in apertural regions of the tetrads and is thickest



Figures 11–14. *Takhtajania perrieri* (TEM micrographs). —11. Section through the center of a tetrad, with the interseptal zone of fusion forming a space near the center (scale bar = 1 μm). —12. Median section of most of a pollen grain in a tetrad passing through the center of an apertural papilla (scale bar = 5 μm). —13. Section through part of the annulus of a pollen grain with an asterisk indicating the center of the lamellated endexine (scale bar = 1 μm). —14. Section through part of the wall of an apertural papilla with underlying peripheral cytoplasm (scale bar = 1 μm).

near the exposed fringes of the pollen grains, where it is 0.5–1.0 μm thick and of similar thickness to the columellae and tectum (Fig. 9). It decreases in thickness toward the distal aperture of each pollen grain (Fig. 9). In septal parts (where the members of a tetrad are contiguous), the foot layer is thinner and measures ca. 0.1–0.4 μm . The inner surface of the foot layer is smooth to undulate (Figs. 9–11). Coherence between members of a tetrad is achieved by fusion of short columella-like elements extend-

ing from the foot layers of adjacent pollen grains (Figs. 9–11). In a few places there are small breaks in the foot layer in septal regions, which are “plugged” by endexine in mature tetrads (Fig. 10).

Beneath the foot layer is an endexine that is considerably thinner than the foot layer, except near the aperture (Figs. 9, 12). In septal regions, it is approximately one-third the thickness (0.1–0.2 μm) of the foot layer and even at low magnifications is readily distinguishable by its greater electron den-

sity (Figs. 9–11). In extraseptal regions, excluding the annulus, it is ca. 0.2–0.3 μm in thickness. It reaches a comparatively massive thickness of up to 3 μm in the annulus region, and here it is made up of compressed lamellar elements more or less tangentially aligned (Fig. 13). Near the external fringes of the annulus and somewhat beyond this, the endexine has an outer, more homogeneous part and an inner region consisting of irregular globules, presumably sporopollenin, separated by electron-transparent spaces giving it a spongy appearance (Figs. 9, 12).

The intine, which underlies the endexine, is of similar thickness to the latter in septal regions (0.05–0.2 μm) and has a homogeneous appearance. It is usually readily distinguishable from the endexine, even at low magnifications (Fig. 9), because of its lower electron density. As Figure 12 illustrates, extraseptal intine increases dramatically in thickness toward the apertures, where it reaches up to 1.8 μm , and as commonly occurs in other Winteraceae (Pragowski, 1979) it loses its homogeneous appearance. There is a further increase in thickness of the intine in the apertural papilla region to up to 2.4 μm , where the wall appears to consist entirely of intine (Fig. 14). It can be seen that in these thicker regions, outer parts of the intine have inclusions of a vesicular-like nature, which is common in similar regions of many angiosperms. Only the innermost part of the intine appears more or less homogeneous (Fig. 14).

DISCUSSION

It would seem that artifactual splits in the aperture in dried pollen, which had been obtained from the type specimen, similar to that shown in preserved pollen in Figure 5, led Straka (1963, 1975) to describe the pollen of *Takhtajania* as colpate and sometimes trichotomocolpate. Figure 1c in Straka (1963: 357) is a photomicrograph showing a triradiate tear in the aperture membrane, which is labeled as a “trichotomocolpate” aperture. Similarly, Lobreau-Callen (1977: 447) illustrated what was termed a colpate (slit-shaped) aperture in a photomicrograph (plate 1, fig. 4), which is very similar to the torn aperture shown in Figure 5 of the present paper. Pragowski (1979: 19) also noted apertures were different from other Winteraceae in their great variation in shape “ranging from pori to colpi.” It is concluded, therefore, that previous reports of these varied types of apertures in *Takhtajania* are incorrect, and that it resembles other members of the family in possessing round or somewhat oval apertures. The study by Lobreau-Callen

(1977) was the only previous one to illustrate pollen of *Takhtajania* under SEM, and two of his illustrations (plate 2, figs. 1 and 4) do show a bulging apertural membrane, despite the fact that pollen was obtained from dried herbarium material. It is unfortunate that it has become well established in the literature that *Takhtajania* pollen is sometimes trichotomocolpate (trichotomosulcate), but one can appreciate the limitations imposed on previous workers when studying pollen from a type specimen collected in 1909. On the other hand, true trichotomocolpate apertures are well defined. For example, the recently discovered genus *Anacostia*, a new basal angiosperm from the early Cretaceous of North America and Portugal, has some pollen grains with clearly delimited and attractively ornamented trichotomocolpate apertures (Friis et al., 1997).

The present investigation supports previous studies that *Takhtajania* has considerably larger tetrads than other members of the family whose pollen has been examined. Endress et al. (2000 this issue) suggested that the presence of these large tetrads may indicate polyploidy, as indicated for some other Winteraceae by Hotchkiss (1955). Straka (1963) stated that the acetolyzed pollen tetrads were 60 μm in diameter; Lobreau-Callen (1977) noted their mean diameter was 57.4 μm , without citing the range of sizes; and Pragowski (1979), who gave mean and size range for the pollen of most other Winteraceae examined, gave a single size of 65 μm diameter for the acetolyzed tetrads, presumably because of the limited material available. The range of tetrad size obtained in the current study (65–83 μm) extends the upper limits of the size range, but no tetrads were found as small as those measured by Straka (1963) and Lobreau-Callen (1977). The mean (74 μm) is considerably higher than that given by Lobreau-Callen (1977). It should be emphasized that acetolysis can increase the size of pollen units by 30% or more, and the extent of the increase may depend on methods of acetolysis used (D. C. Mildenhall, pers. comm. 1999). In fact, tetrads of *Takhtajania*, which had been dried by the critical point method for SEM (Figs. 1, 2, 4, 5, 7) had a diameter (excluding the apertural papillae) averaging ca. 47 μm . It is highly probable that the tetrads of other Winteraceae undergo a similar increase in size with acetolysis. Thus, *Pseudowintera colorata*, which had tetrads with a mean diameter of 50 μm following acetolysis (Pragowski, 1979), measured ca. 35 μm under SEM, when material has been dried by the critical point method (unpublished pers. obs.).

Lobreau-Callen (1977) and Pragowski (1979)

made detailed comparisons between the pollen of *Takhtajania* and other genera in the family. Lobreau-Callen (1977) concluded that based on its structure and sculpture, its pollen is closest to that of *Belliolum*, from which *Takhtajania* can be distinguished by the difference in size of perforations in the internal walls (septae), which are large in *Belliolum*. It was subsequently found for several genera in the family that if these gaps are still open at the time of pollen grain mitosis and therefore the four members of a tetrad share a common cytoplasm, division into tube and generative cells within each pollen grain is synchronous within a tetrad, e.g., in *Belliolum* (Sampson, 1981). It is probable that pollen grain mitosis is asynchronous within each tetrad of *Takhtajania*, because the small and infrequent gaps in the ectexine forming the septae are plugged with endexine, which is formed before division—at least in those species that have been investigated. On the other hand, species with synchronous division have, in older tetrads, the septal gaps plugged with intine, which is formed subsequent to pollen mitosis (Sampson, 1981), or large gaps may remain open in mature tetrads, as illustrated by Pragłowski (1979) for *Bubbia howeana* (F. Muell.) Tiegh. Assuming that *Takhtajania* has asynchronous pollen mitosis, it shares this feature with *Pseudowintera* and *Drimys*. Whether or not this indicates a relationship between these three genera depends on whether asynchronous mitosis, the adaptive significance of which is not obvious, has evolved independently in these taxa. Furthermore, this feature has not been investigated in all species in the family, and future studies may demonstrate that it is not consistent within a genus. For example, although asynchronous division occurs in all three species of *Pseudowintera*, only one species of *Drimys* has been examined (Sampson, 1981). It has been suggested that the asynchronous type has evolved from the synchronous (Sampson, 1981).

In contrast to other Winteraceae, *Drimys*, *Takhtajania*, and *Pseudowintera* share protuberant apertural papillae, which may or may not indicate a relationship between the genera, depending on whether or not this characteristic evolved independently in these three genera. Bailey and Nast (1943) noted that van Tieghem (1900), who studied pollen of all genera (excluding *Takhtajania*), although he provided no illustrations, found that the pollen of the three New World species of *Drimys* he examined formed protuberant papillae when moistened, in contrast to *Tasmannia* (*Drimys* sect. *Tasmannia*), *Pseudowintera*, *Bubbia*, *Belliolum*, *Exospermum*, and *Zygogynum*. Bailey and Nast (1943) confirmed these results. However, fresh and pre-

served pollen of all three species of *Pseudowintera* have the papillae (Fig. 8). Both *Takhtajania* and *Pseudowintera* possess an annulus that is verrucate (Figs. 3, 8) with smaller verrucae in *Takhtajania*, in contrast to the comparatively smooth-surfaced annuli illustrated for species of *Drimys* (sensu Smith, 1969) by Lobreau-Callen (1977) and Pragłowski (1979). Tetrads of *Pseudowintera* differ from those of *Takhtajania* in generally lacking expanded tips to their columellae where they touch the foot layer and in possessing numerous small perforations in the tectum near their external boundaries (Fig. 8).

Pragłowski (1979), while agreeing that *Takhtajania* pollen differs considerably from that of *Bubbia*, the genus in which *Takhtajania perrieri* had first been placed (Capuron, 1963), disagreed with the conclusion of Lobreau-Callen (1977) that it was closest to pollen of *Belliolum*. Pragłowski (1979) questioned the value of the ratio between the width of muri and the diameter of bacula (columellae) used by Lobreau-Callen (1977) for intergeneric segregation and concluded its pollen was closest to that of *Drimys* (syn. *Drimys* sect. *Drimys*). Lobreau-Callen (1977) also had noted similarities between *Takhtajania* and *Drimys* pollen. Coetzee and Pragłowski (1988) described two types of fossil Winteraceae pollen resembling *Tasmannia* and *Bubbia* from the Miocene of South Africa. This discovery and the Early Cretaceous occurrence of Winteraceae pollen in Israel (Walker et al., 1983) led them to suggest that the Winteraceae had a West Gondwanan origin and an early differentiation, possibly in Africa, before migration to Australasia and Madagascar. They suggested furthermore that a dispersal route from the south could probably explain the close resemblance between the pollen of *Takhtajania* and *Drimys* of the New World. Doyle et al. (1990a) noted that extinct relatives of the Winteraceae (*Afropollis*) were an important component of Early Cretaceous tropical floras and extended into Laurasia, and commented that their present austral temperate distribution was attained later. The winteraceous affinity of *Afropollis* has, however, been questioned by Friis et al. (1999).

Ultrastructural detail in pollen of the Winteraceae (e.g., intine and endexine structure, endexine fine structure) does not seem to differ significantly between genera (Pragłowski, 1979, and unpublished pers. obs.). However, further studies are needed to confirm this, utilizing freshly collected pollen and TEM fixation techniques.

Table 1, which includes information from Pragłowski (1979), the present study, and unpublished personal observations, summarizes a number of pol-

Table 1. Some pollen features of Winteraceae. Abbreviations: T = tetrad, M = monad, * = includes *Zygogynum acsmithii* with tetrad pollen, N.A. = not applicable

Genus	<i>Takhtajania</i>	<i>Pseudowintera</i>	<i>Drimys</i>	<i>Belliolum</i>	<i>Bubbia</i>	<i>Tasmania</i>	<i>Zygogynum</i>	<i>Exospermum</i>
Tetrad diameter (µm)	65–83	36–55	34–55	34–48	33–50	32–39	32–51	37–43
Are tetrads circular in outline?	No	No	No	No	No	No	No	Yes
Are apertures surrounded by an annulus-like region?	Yes	Yes	Yes	Yes	Yes	No	No, T Yes, M	No
Do apertures have protruberant papillae?	Yes	Yes	Yes	No	No	No	No	No
Exine structure	reticulate	reticulate	reticulate	reticulate	reticulate	reticulate	reticulate, T tectate-perforate to micro-reticulate, M*	tectate-perforate to micro-reticulate
Number of lumina (1 grain-lateral view)	25–30	13–20	13–26	8–20	10–20	10–20	40–100	>100
Columellae shorter than thickness of the tectum?	No	No	No	Yes	No	Yes	No	No
Height/width ratio of muri	1:1–3:2	3:1	2:1	4:1	2:1 or 3:2	3:2 or 2:1	tetrads 3:2 monads, N.A.	N.A.
Pollen mitosis synchronous /tetrad	No(?)	No	No	Yes	Yes	Yes	Yes	Yes
Columellae appear two-layered because of thicker distal segments?	No	No	No	No	No	No	No	Yes
Maximum thickness of sexine (µm)	6.0	2.5–4.0	2.5–5.0	2.0–4.5	2.5–3.5	2.0–3.0	2.0–4.0, T 1.5–2.5, M	3.0
Maximum thickness of nexine (µm)	1.5	1.5	1.0	1.0	1.0	0.5	1.0, T 0.5–2.0, M	0.5

len characters of the genera. Assuming that some or all similar characters are not the result of convergent evolution, the pollen of *Takhtajania* most closely resembles that of *Pseudowintera* and *Drimys*. Endress et al. (2000) reached somewhat different conclusions when considering the total evidence of floral features and considered that *Takhtajania* fits best in the *Pseudowintera*–*Zygogynum* (including *Bubbia*, *Belliolum*, and *Exospermum*) clade, “which is sister to the *Tasmannia*/*Drimys* clade.” Hopefully, further studies, including those using molecular data, will provide further information on the relationships between *Takhtajania* and other Winteraceae.

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